

Cerasuolo et al-LUCASS(JXB-resubmit)-EN.docx

1 **Development of a sink-source interaction model for the growth of SRC willow**
 2 **and *in silico* exploration of $G \times E$ effects**

3

4 Cerasuolo M^{1*}, Richter GM^{1‡}, Richard B¹, Cunniff J², Girbau S², Shield I², Purdy S³,
 5 and Karp A²

6 ¹Sustainable Soils and Grassland Systems Department, Rothamsted Research,
 7 Harpenden, Herts AL5 2JQ, UK

8 ²Agroecology Department, Rothamsted Research, Harpenden, Herts AL5 2JQ, UK

9 ³Institute of Biological Environmental and Rural Sciences (IBERS), Aberystwyth
 10 University, Plas Gogerddan, Aberystwyth, Ceredigion SY23 3EE, UK

11

12 **Running title:** Environmental Effects on Willow Genotypes

13

14 **Highlight:**

15 The process-based model LUCASS gave insights into the sink-source control of
 16 willow growth and identified key parameters to predict the performance of
 17 perennials in different environments.

18

Part	Max word number	submission
Abstract	250	218
Total main body + references	10,000	8079
Figures (captions)		8 (357)
Tables		3 (1169)
SI (Model description)		
References		87 (2534words)

19

20 [‡]**Corresponding author:** goetz.richter@rothamsted.ac.uk

21 Telephone: +44 (0)1582 763 133; Fax +44(0) 1582 760 981

22

23 ***Current address:** Department of Mathematics, University of Portsmouth, Lion Gate
 24 Building, Lion Terrace, Portsmouth, Hampshire PO1 3HF, UK

25

26 **Abstract**

27 Identifying key performance traits is essential for elucidating crop growth processes
28 and breeding. In *Salix* spp. genotypic diversity is being exploited to tailor new
29 varieties to overcome environmental yield constraints. Process-based models can
30 assist these efforts by identifying key parameters of yield formation for different
31 Genotype \times Environment combinations. Here, four commercial willow varieties
32 grown in contrasting environments (West and South-East UK) were intensively
33 sampled for growth traits over two 2-year rotations. A sink-source interaction model
34 was developed to parameterise the balance of source (carbon capture/mobilization)
35 and sink formation (morphogenesis, carbon allocation) during growth. Global
36 sensitivity analysis identified day length for the onset of stem elongation as most
37 important for yield formation, followed by various “sink > source” controlling
38 parameters. In coastal climate the chilling control of budburst ranked higher
39 compared to the more eastern climate. Sensitivity to drought, including canopy size
40 and rooting depth, was growth-limiting in the South-East but not in the west of the
41 UK. Light use efficiency increased during perennial maturation of the crop,
42 distinguishing varieties according to canopy size and emphasized quantum efficiency
43 at low light intensity as key to assimilation. However, on average sink parameters
44 were more important than source. The Genotype \times Environment pairings described
45 with this new process model helped to identify parameters of sink-source control for
46 future willow breeding.

47

48

49

50 **Keywords:** *Salix*; modelling; carbon allocation; sink-source interaction; sensitivity
51 analysis; genotype

52

53 **Introduction**

54 Yield improvement is an important objective in the development of woody biomass
 55 feedstocks from short-rotation coppice (SRC) (Karp and Shield, 2008; Volk *et al.*,
 56 2006). Poplar (*Populus* spp.) and willow (*Salix* spp.) are comparatively young in
 57 their domestication (Karp *et al.*, 2011; Stanton *et al.*, 2014) and pedo-climatic
 58 adaptation (Aylott *et al.*, 2008; Toillon *et al.*, 2013). However, yields have been
 59 doubled by breeders selecting mainly for total biomass, stem traits and disease
 60 resistance (Karp *et al.*, 2011). Traits associated with vigour (Kauter *et al.*, 2003;
 61 Verlinden *et al.*, 2013; Volk *et al.*, 2006; Weih and Nordh, 2005), development
 62 (Toillon *et al.*, 2013; Verwijst *et al.*, 2012), photosynthesis (Andralojc *et al.*, 2014;
 63 Robinson *et al.*, 2004) and water use efficiency (Deckmyn *et al.*, 2004; Weih and
 64 Nordh, 2002) are now also being incorporated. However, experimental evidence for
 65 carbon assimilation (source formation) and its linkage to allocation (sink formation)
 66 to above- (AGB) (Bullard *et al.*, 2002b; Guidi *et al.*, 2009; Laureysens *et al.*, 2003)
 67 and belowground biomass (BGB) (Heilman *et al.*, 1994; Martin and Stephens, 2006;
 68 Matthews, 2001; Pacaldo *et al.*, 2013; Rytter, 2001) has yet to be integrated.

69 Process-based simulation models are useful tools for integrating knowledge and
 70 assessing the relative importance of traits, particularly in woody perennials with long
 71 growth cycles, where gathering experimental data is time consuming and expensive
 72 (Karp *et al.*, 2014). SRC comprises successive harvest (coppicing) rotations lasting
 73 two to three years, where “re-growth” after harvest occurs from basal buds on
 74 coppiced stools whilst successive “annual growth” before harvest occurs from buds
 75 on the stems. Annual re-growth from reserves was poorly addressed in early models
 76 (Le Roux *et al.*, 2001), despite its importance (Ceulemans *et al.*, 1996; Philippot,
 77 1996). The existing models for SRC treat growth either as source-dependent (“top-
 78 down”), limited by light interception and use efficiency (Tharakan *et al.*, 2008), or as
 79 sink-dependent (“bottom-up”) and influenced by coppice response and carbon
 80 allocation (Deckmyn *et al.*, 2004). For phenological development a simple empirical
 81 canopy model (Deckmyn *et al.*, 2004) was later replaced by a temperature-controlled
 82 budburst model (Deckmyn *et al.*, 2008), and adapted for SRC without validation
 83 (Tallis *et al.*, 2013). The need to model temperature control of dormancy, currently
 84 debated in many species (Fu *et al.*, 2012), is also unclear in willow (Savage and
 85 Cavender-Bares, 2011). Indeed, the whole system of yield formation, dormancy

86 break, budburst and start of photosynthesis needs to be integrated with the initiation
87 of stem growth (sink formation).

88 Carbon allocation and sink formation has often been simplified in previous models
89 (Deckmyn *et al.*, 2004) and allocation to BGB reserves ignored, despite its potential
90 importance for regrowth after coppicing (Ceulemans *et al.*, 1996; Tschaplinski and
91 Blake, 1995). Control of early soft wood production by labile carbon allocated to
92 tree reserves (Deckmyn *et al.*, 2008) has recently been observed for SRC (Verwijst
93 *et al.*, 2012). The importance of reserves for regrowth was also shown in perennial
94 forage crops (Schapendonk *et al.*, 1998; Teixeira *et al.*, 2007). For grassland a sink-
95 source interaction model was proposed (Schapendonk *et al.*, 1998) where assimilate
96 allocation is controlled by sink formation. A similar control has been implemented
97 for carbon partitioning in forest models (Fourcaud *et al.*, 2008; Pretzsch *et al.*, 2008).
98 Carbon translocation is important for both, SRC and grass, which show die-back of
99 stems and tillers, respectively. Data from empirical protocols (stem number, length
100 and diameter), used for SRC phenotyping, can be used for the development of a
101 hybrid model, which combines morphometric data with an eco-physiological process
102 model as suggested by (Pretzsch *et al.*, 2008). This is similar to the approach to
103 predict yields of specific willow clones proposed by (Amichev *et al.*, 2011).

104 To simulate growth processes sufficiently well for use in willow breeding, there is a
105 clear need to derive an integrated model that adequately incorporates key
106 phenological processes and morphogenesis controlling AGB, whilst also taking into
107 account BGB and the influence of reserves. In particular, it is important to integrate
108 new experimental evidence, assess sink- and source-limitations, rank genotype-
109 specific parameters and identify the most important ones to focus breeding efforts.

110 To address these challenges we developed a sink-source interaction model, LUCASS
111 (Light Use and Carbon Allocation in Salix Species) in which phenology controls
112 growth and yield formation. This model describes and predicts the growth of four
113 commercial willow genotypes. The model was calibrated for potential and water-
114 limited production using detailed field data at two different sites in the UK. Key
115 parameters for yield formation, across varieties and in different environments, were
116 identified using a global sensitivity analysis. Finally, the model was validated against
117 independent datasets.

118 **Materials and Methods**

119 **Field experiments**

120 Detailed observations describing plant growth were recorded in two identical field
 121 trials laid out in a randomised block design consisting of four blocks (Cunniff *et al.*,
 122 2015). Each block contained four commercial *Salix* varieties (Endurance (*S.*
 123 *redheriana* \times *S. dasyclados*), Resolution (multiple parental crosses of *S. viminalis* \times
 124 *S. schwerinii*), Terra Nova ((*S. viminalis* \times *triandra*) \times *S. miyabeana*) and Tora (*S.*
 125 *schwerinii* \times (*S. viminalis* \times *viminalis*)) in individual plots of 224 m². Details can be
 126 found in Table 1 in Cunniff *et al.* (2015). These varieties were grouped according to
 127 phenotype of broad-leaved, closed canopy (Endurance, END; Terra Nova, TN) and
 128 narrow-leaved, open canopy (Resolution, RES; Tora, T). The crops were planted in
 129 double rows (16,000 cuttings ha⁻¹) in May 2009 and coppiced in January 2010, 2012
 130 and 2014. Destructive and non-destructive measurements of AGB and BGB traits
 131 were taken from respective plot areas during two successive 2-year rotations (R1,
 132 first rotation, 2010-2011; R2, second rotation, 2012-2013) to populate an extensive
 133 database for research and model development.

134 *Locations*

135 The experiments used for model parameterisation (where previous data were not
 136 available), calibration and internal evaluation were located in south east England
 137 (51.82°N, 0.38°W) at Rothamsted (ROTH) and Aberystwyth (ABER) in Wales
 138 (52.4139°N, 4.014°W). Soils were characterised as a silty clay loam (chromic
 139 Luvisol) and a shallower sandy silt loam (eutric endoleptic Cambisol), respectively.
 140 Final yield data, available for three of the varieties, collected from separate trials at
 141 Long Ashton (LARS) in Somerset, England (51.43°N, 2.65°W) and ROTH between
 142 2001 and 2010 were used for external model validation. LARS soil was classified as
 143 a coarse loam over clay (stagnogley) to clay (argillic Pelosol), see Table S1.

144 The long-term averages characterize ROTH as drier with a higher probability of
 145 water stress (704 mm, 9.3 °C) than ABER (1038 mm, 9.7 °C). Site-specific hourly
 146 weather data were recorded. The 1st rotation (R1, 2010-2011) was drier, 2nd rotation
 147 (R2), especially 2012, was wetter than the long-term average (**Figure S1; Table S2**).

Over all years, annual radiation at ROTH was about 20% higher and the temperature range (T_{\min}/T_{\max}) wider than at ABER (Table 1).

<Table 1>

Phenotyping

Budburst was recorded annually (2010 to 2013), and buds were scored on 10 trees from early February twice weekly until bud swelling then checked daily. Adapting a 7-point scale (Weih, 2009), budburst was defined as green leaf tips (<5mm) visible. Senescence was scored weekly through September to October using 10 trees per treatment and block, adapting a 7-point scale (Fracheboud *et al.*, 2009), defining its onset as >25% yellow/brown and <10% abscised leaves.

Plant architecture (height, stem length and diameter, and number of stems) was assessed on two pairs of trees, randomly chosen from the non-destructive area of each plot. Leaf area indices (LAI) were estimated at ROTH twice monthly using the SunScan Canopy Analysis system (Delta-T Devices Ltd, Cambridge, UK). LUE was estimated from simulated cumulative woody stem biomass and absorbed photosynthetic active radiation (APAR) based on calibrated LAI.

Carbon allocation rates to AGB and BGB components were determined during the first rotation (2010-2012) by destructively sampling two complete trees per plot at key phenological stages (Cunniff *et al.*, 2015). Stool and roots were excavated to a depth of 0.3m, which is likely to represent >90% of the BGB (Pacaldo *et al.*, 2013). Destructive measurements of leaf weight and area were recorded (Cerasuolo *et al.*, 2013). During the second rotation (2012-2013) the number of destructive samples was reduced to twice a year and final yields were assessed after each 2-year coppicing cycle (Cunniff *et al.*, 2015).

Model description

The process-based willow growth model LUCASS (**Figure 1**) simulates development and growth of *Salix* spp., considering phenological (budburst, growth, senescence and dormancy) and morphological plant development (sink formation), and light interception, photosynthesis and respiration (source formation). The AGB and BGB organs (leaves, branches, stems, and stool and roots, respectively) are

178 considered as sinks and the carbon allocation to these sinks is phenologically
 179 controlled and balanced within the sink-source interaction model (Schapendonk *et*
 180 *al.*, 1998). The sinks are phenotypically dimensioned by stem and leaf numbers,
 181 their respective elongation rates and specific dry matter densities, which define the
 182 carbon demand from a common source pool fuelled by photosynthesis and
 183 mobilisable reserves.

184 <Figure 1>

185 These processes are controlled by external variables (global radiation, air
 186 temperature and water availability), provided by an environmental modelling
 187 framework (Richter *et al.*, 2006) that simulates the water and energy balance.
 188 LUCASS follows a bottom-up approach where light interception, photosynthesis and
 189 respiration (Goudriaan and van Laar, 1994) are simulated with an hourly time step as
 190 part of the energy balance. Assimilate allocation to biomass components (leaf,
 191 branch, stem, stool and roots) and respective reserve pools are calculated daily.
 192 Source-sink carbon flows are considered independently, however, carbon from
 193 senescing biomass (leaves, branch die-back) is translocated to the reserves.

194 *Phenology*

195 LUCASS simulates the multi-annual cycle of phenological development at the centre
 196 of process control (Figure 1): budburst and leaf emergence, growth of individual
 197 organs, senescence and stem die-back, and dormancy to control the onset and
 198 duration of carbon capture (source formation) and its allocation to various sinks, as
 199 done in grape vine (Vivin *et al.*, 2002).

200 *Budburst, leaf emergence and elongation*

201 Similar to earlier work (Tallis *et al.*, 2013) the budburst was simulated combining a
 202 chilling phase followed by a forcing period (Chuine, 2000; Hlaszny *et al.*, 2012).
 203 Budburst dates were calculated (eq. S1) using daily mean air temperature (T_{avr}), a
 204 half-efficiency temperature (T_C) and a chilling threshold, C_r ; both, T_C and C_r , were
 205 estimated using genotype-specific budburst data. The other parameters were adapted
 206 from (Hlaszny *et al.*, 2012). Chilling unit accumulation started with senescence
 207 during the previous season. In keeping with the known biology (Rinne *et al.*, 2011)

negative chill units (C_u) accumulate during endo-dormancy until plants reach C_r as in (Cesaraccio *et al.*, 2004). At this point the model plants enter eco-dormancy, an inactive “standby” phase, to accumulate daily forcing (anti-chill) units (C_a), which results in budburst when $C_r + \sum C_a \geq 0$.

Leaf emergence rate was calculated as suggested by (Porter *et al.*, 1993) and adjusted by photoperiod, water availability and level of reserves (eq. S2). The leaf emergence declined exponentially over the year. Potential leaf elongation rate was considered dependent on average temperature and day length (Mcdonald and Stadenberg, 1993), modified for plant age (Robinson *et al.*, 2004) and water stress (eq. S3).

218 *Senescence and canopy duration*

The model considers leaf senescence as a function of age (accumulated thermal time, μ_T), shading (μ_s , LAI >3) and water stress (μ_w). The start of senescence depends on a threshold day-length, while the date of growth cessation (budset) is modelled as a function of accumulated thermal time; both values were estimated using experimental data (senescence score; end of stem extension) collected at ROTH and ABER during R1.

225 *Stem and woody biomass development*

Experimental evidence suggested modelling the onset and rate of stem extension as a function of day length (eq. S5) with a developmental switch considering the base temperature for stem elongation ($T_{bSE} = 10^\circ\text{C}$). This is in contrast to grass models in which leaf and stem extension are determined by temperature (Hoeglind *et al.*, 2005; Schapendonk *et al.*, 1998). The dynamics of stem number is described by a function of the number of initial buds, which form stems and their calibrated die-back rate. The demography of leaves (Porter *et al.*, 1993) and stems (Hoeglind *et al.*, 2005; Schapendonk *et al.*, 1998) was incorporated in order to consider the empirical evidence for re-growth after coppicing, e.g. die-back (self-thinning) of stems. The model does not consider plant mortality (Bullard *et al.*, 2002b).

236 *Sink formation*237 *Leaf area and biomass*

238 Total leaf area is a function of leaf number, size and shape, scaled to LAI (eq. S4).
 239 Initially, willow varieties produce a large number of small shoots in order to rapidly
 240 increase leaf area. These branches were treated as “super-leaves” (long leaves whose
 241 area is equal to the cumulative area of leaves on the branch), whose growth rate
 242 follows the normal-leaf emergence and elongation rate. The leaf area is converted to
 243 leaf biomass using a dynamic specific leaf area ($SLA_{min/max}$; (Schapendonk *et al.*,
 244 1998)) that accounts for increasing leaf thickness and variable level of reserves. In
 245 the model mobilisable leaf carbon is translocated during senescence.

246 *Stem and woody biomass*

247 Potential stem elongation is modelled using a linear function of day length
 248 multiplied by a Heaviside function for the effect of daily average air temperature
 249 (Powers *et al.*, 2006) (eq. S5).

250 The woody growth potential is expressed in terms of total dry biomass production,
 251 which was computed from the average stem volume and specific stem dry weight,
 252 multiplied by the observed/simulated number of stems still alive. The stem volume
 253 depends on stem length and diameter/height ratio (m_{DH} ; eq. S6) modified by a shape
 254 parameter η_{St} (eq. S7), as stems are not exact cylinders.

255 *Belowground biomass*

256 The stool and coarse and fine roots are the components of BGB modelled defining
 257 respective elongation rates, radial extension and specific densities. Parameters define
 258 allocation (de Neergaard *et al.*, 2002) and turnover (Rytter, 2001) rates of fine root
 259 dry matter.

260 *Source formation*261 *Light interception*

262 The genotype specific light interception is described by a pseudo-3D architectural
 263 model (Cerasuolo *et al.*, 2013), which defines horizontal and vertical spatial

264 distribution of leaves in a gap fraction model, characterising LAI by clumping (Ω)
 265 and profile shape (η) factors. The LAI is computed daily and the cumulative LAI is
 266 considered as $\Omega \times L_c(z)$, where $L_c(z)$ is the distribution of leaf area over the canopy
 267 depth (z). The light interception module describes the effect of canopy clumping on
 268 both, direct and diffuse radiation (De Pury and Farquhar, 1997). The extinction
 269 coefficient for the diffuse radiation is calculated according to (Goudriaan, 1988),
 270 with weighted contributions from the three zones of a standard overcast sky. To
 271 simulate light interception the canopy is divided into five layers, which are either
 272 uniformly or asymmetrically distributed. Within each layer the ratio of sunlit/shaded
 273 leaf area is calculated to estimate the vertical variation of photosynthesis inside the
 274 canopy.

275 *Photosynthesis and carbon pools*

276 Photosynthesis is computed as the assimilation rate of carbon dioxide (CO_2) using
 277 the maximum between an exponential function of the intercepted energy (absorbed
 278 photosynthetic active radiation; APAR) and its potential absorption, modified by
 279 CO_2 air concentration and air temperature (Goudriaan and van Laar, 1994). The
 280 effect of soil water availability on stomatal conductance and reduction in CO_2
 281 absorption is represented using a logistic function to describe the reduction of
 282 photosynthesis with decreasing relative soil water content (Sinclair, 1986).

283 Three different biochemical pools are simulated: First, a source pool of available
 284 carbohydrates (C_{av}) composed of photosynthetic assimilates and remobilised
 285 reserves used for growth and maintenance processes. Second, a source/sink pool of
 286 mobilisable carbohydrate reserves (e.g. starch) in leaves, wood and stool. Finally, the
 287 sink pool of structural biomass, divided into *AGB* (stems, branches and leaves) and
 288 *BGB* (stool, coarse and fine roots).

289 *Sink-source interaction*

290 *Carbon allocation*

291 The allocation of C_{av} is modelled as a combination of a sink-source balance and a
 292 hierarchical cascade (leaf > stem \approx [stool & root]). The respective sink strengths
 293 result from genetically determined growth potentials (see above) defined by the

294 maximum rate of each organ's dry matter accumulation and turnover (Genard *et al.*,
295 2008).

296 The total source (C_{av} ; eq. 1a) to satisfy sink demands is calculated as the net daily
297 integral of the difference between hourly leaf photosynthesis (CH_2O) and
298 maintenance respiration of the respective tree organs (R_t ; eq. 1b), plus the
299 mobilisable reserves from leaves (Lf_{Res}), woody biomass (W_{Res}), and stool (Stl_{Res}):

$$300 \quad C_{av} = CH_2O - R_t + Lf_{Res} + W_{Res} + \alpha \times Stl_{Res}, \quad (1a)$$

$$301 \quad R_t = (m_{Lf} \times Lf + m_B \times B + m_{Stl} \times Stl) \times Q_{10}^{\frac{T_{avr} - T_{Q10}}{10}} \quad (1b)$$

302 A fraction of Stl_{Res} ($\alpha = 0.04$) can be mobilised for 20 days after budburst ((Deckmyn
303 *et al.*, 2008) ANAFORE Manual). If new assimilates exceed sink demands
304 (Schapendonk *et al.*, 1998) the emerging surplus of assimilates is allocated to the
305 reserve pools. The available carbohydrates for aboveground biomass (AGB_{av}) are
306 converted into leaf (LfB) and woody stem biomass (WSB) using their respective
307 conversion factors (Penning de Vries *et al.*, 1983) and potential sink increases:

$$308 \quad LfB = AGB_{av} \times LfGrPt / ShGrPt, \quad (2a)$$

$$309 \quad WSB = AGB_{av} \times SGrPt / ShGrPt. \quad (2b)$$

310 Here $ShGrPt$ represents the total shoot growth potential, and $LGrPt$ and $SGrPt$ the
311 leaf and stem growth potentials, respectively.

312 C_{av} is partitioned between AGB_{av} and BGB_{av} using constant potential allocation
313 coefficients, derived from the experimental evidence. These allocation coefficients
314 change with stool size to account for increasing plant vigour during establishment
315 and drought to increase root growth for better resource capture (Goudriaan and van
316 Laar, 1994).

$$317 \quad StlB = BGB_{av} \times StlGrPt / BGGrPt \quad (3a)$$

$$318 \quad RtB = BGB_{av} \times RtGrPt / BGGrPt \quad (3b)$$

319 Stool and roots are assumed to turnover with different rates; stools are set to have a
320 longevity, which corresponds to the stand/plant life-time (Bullard *et al.*, 2002b),
321 whilst fine roots are set to a high annual turnover rate (Rytter, 2001).

Consecutively, C_{av} is allocated to the plant organs according to their respective sink strengths, defined by LAI and SLA, wood volume and density, stool mass, root growth and turnover. Daily carbon allocation is, therefore, either limited by C_{av} , or by the effective sink demand of assimilates (potential growth). At each time step, LUCASS balances the gain and consumption of carbon, estimates the conversion of C_{av} into growth, and calculates the produced biomass (g m^{-2} upscaled to kg ha^{-1}).

Effects of the environment

The soil hydrology is modelled using an energy balance approach combined with a two layer soil water module (Richter *et al.*, 2006). The energy fluxes at the canopy surface are controlled by crop characteristics (LAI, stomatal resistance, canopy height), climatic variables, and soil hydraulic properties (Table s1). The rooting depth is dynamic and calculated using a constant crop specific root advancement coefficient and a maximum rooting depth. The soil water balance, transpiration and water uptake, are calculated using the Penman-Monteith equation. The plant water stress variable, k_{ws} , is described by a non-linear, logistic function (eq. S2c) in dependence of the relative water content between minimum and maximum plant available soil water (Sinclair, 1986). Its curvature is determined by the water stress parameter, WSP (Table 2), which was calibrated using R1 data at ROTH. A/BGB partitioning is modified according to soil water availability (van Laar *et al.*, 1992).

<Table 2>

The effects of water stress on leaf emergence and elongation rates, and stem and leaf mortality are also considered as a function of k_{ws} and respective potential rates. Buds and branches follow the same dynamics as leaves, but the mortality rate of branches is assumed to be 10 times lower than that of leaves. The mortality rate of stems is also computed as the sum of natural turnover and death rate caused by water and shading stress, however, stem mortality is less than that of leaves (**Table S2**).

Calibration and parameter ranking

The model inputs divide into environmental variables and process parameters: (i) field location (longitude, latitude etc.) and soil characteristics; (ii) management data (irrigation, harvest days, number of years per growth-cycle); (iii) [hourly] weather

352 data, e.g. solar radiation, mean air temperature, wind speed and direction, rainfall
353 and air humidity; and (iv) genotype-specific growth parameters.

354 *Model calibration*

355 The parameters of the growth model were calibrated using genotype-specific
356 experimental data where values from the literature were not available (**Table 2**).
357 Process-specific evidence was used to calibrate development and morphology either
358 through direct measurements (e.g. leaf emergence and senescence) or through
359 parameter estimation involving model data fitting (e.g. budburst, stem height and
360 stem diameter). Model cross-validation was performed using time-series of the
361 variables not used for calibration (e.g. canopy height, stem biomass). The
362 photosynthesis parameters (Bonneau, 2004) were calibrated to match total biomass
363 production and turnover.

364 Parameters of the budburst model (eq. S1) were calibrated using ROTH data from
365 the first rotation cycle (2010-11), while parameters for stem height/diameter
366 relationships were estimated using data from both locations (ABER and ROTH,
367 2010-11). LUCASS (remaining parameters) was calibrated for potential productivity
368 using data from ABER assuming that water was unlikely to limit growth and carbon
369 partitioning. The flux parameters for carbon allocation were calibrated using
370 morphological components of AGB (leaf and stem weight) and BGB (stool and fine
371 root weight). In a final step, water stress effect on biomass production was calibrated
372 using time series of data collected at ROTH (e.g., LAI).

373 *Sensitivity analysis*

374 A global sensitivity analysis (SA) was performed for all varieties and both sites for
375 potential (no water stress, NWS) and actual (water stress, WS) growth, and the
376 model response was determined for the first and second coppice rotation (R1, R2).
377 The aim was to understand which growth parameters had a significant impact on
378 final yield, whether it changed with the environment, age of stand or phenotype. All
379 of 78 parameters (Table 2) were varied in a one-at-a-time modus using the Morris'
380 method (Morris, 1991). Assuming that all parameters were normally distributed
381 (Richter *et al.*, 2010) the window of their variation was set to a respective standard
382 deviation of 10%. The estimated average response strength (μ) for each parameter

represents its overall effect on the model outcome (e.g. final yield). Its standard deviation (σ) represents the response spread estimating higher order effects (non-linearity, parameter interactions). Both μ and σ were calculated over six different trajectories (individual one-parameter-at-a-time simulations) and using six levels (granularity of the explored parameter space) (Richter *et al.*, 2010).

Data analysis and model validation

Data were analysed with GenstatTM 14 (Payne *et al.*, 2011) to examine the influence of location and varieties using a two way Analysis of Variance (ANOVA). Linear regressions were performed using Sigmaplot (version 12.0, 2011). The model was validated against yield data from the second growth cycle at ROTH, and independent datasets for three of the four varieties at LARS and ROTH. The goodness of simulations to match experimental data for the two dedicated trials was characterised with the Residual Mean Square Error (RMSE). The coefficient of determination, the model efficiency (ME), RMSE, bias (Mean difference, MD) and r^2 were calculated according to (Smith *et al.*, 1997).

Results

All following results fall into a distinct pattern due to significantly different climatic conditions during the two rotations where R1 was distinctly drier than R2, which translated into high water stress, especially in 2010, and low water stress, especially in 2012. These conditions were exacerbated by site differences and reached almost potential (NWS) conditions in ABER during 2012 whilst ROTH had strong WS conditions during R1 growth.

Sensitivity analysis

Identification and ranking of key parameters

The heat map details (**Figure S2**) showed a clear pattern of high sensitivity under potential (NWS) and low water stress (R2) growing conditions which translated clearly into the aggregated averages (Figure 2). Considering a model response threshold of about 1000 kg ha⁻¹ per 10% parameter change (4 to 5% yield potential), the SA revealed that yields were affected by up to 20 parameters (under NWS). Under conditions of growth-limiting WS the number of parameters with significant

effects on yield dropped to less than 10. However, these ranked consistently high when considering the average response to their variation across sites (ABER, ROTH), age (R1, 2) and canopy phenotype. Model sensitivity was higher in the second (R2) than in the first rotation (Figure 3) most likely due to lower water stress. Differences between sites were overall small and affected only few parameters (day length associated with buds turning into branches dl_{BtoBr} ; A/BG partitioning, ρ_{AB} , and quantum efficiency, φ_{pot}). Most of these parameters reflected experimental evidence and measurable crop traits defining sinks and sources.

<Figure 2>

Sink formation – Pheno-morphology

The onset of stem elongation (dl_{0SER}) was identified as the overall most important yield determining (phenological) parameter at both sites and for all conditions. It was followed by closely related morphological sink determinants, like stem elongation rate (m_{SER}) and diameter/height coefficient (m_{DH}). The fraction of total biomass allocated to AGB (ρ_{AG}) also ranked among the strongest effects, emphasizing the importance of A/BGB partitioning. The fraction allocated to roots (ρ_{Rt}) had an equally large effect (0.7 to 2.3 Mg ha⁻¹). These sink parameters had a most stable ranking across most of the subsets of the SA; exceptions were rank changes for ρ_{AG} with site and phenotype.

Phenological parameters that determine budburst (chilling requirement C_r ; base temperature T_c) showed a very inconsistent and contrasting behaviour. C_r ranked overall higher for potential than water-limited growth which was also reflected in its higher rank in the wet second rotation. Differences between sites were marginal but both parameters were slightly more important for ABER than ROTH (Table S4); however, C_r ranked on average slightly higher for the open canopy phenotype (Figure 2).

Source formation

Source-related parameters (light interception, photosynthesis) were on average less sensitive than sink-related parameters. Parameters of canopy structure (Ω ; η) were identified as important under potential (2.3 and 1.6 Mg ha⁻¹), but not under water-limited production (<0.5 Mg ha⁻¹). On the other hand, parameters determining light

interception, e.g. number of leaves and leaf elongation rate ($> 2 \text{ Mg ha}^{-1}$) ranked consistently high, irrespective of the site, rotation or phenotype. The sensitivity of photosynthesis, quantum efficiency, ϕ_{pot} , was on average more than twice that of A_{max} , emphasizing light conversion at low light levels to be crucial for willow production in the UK. There was a difference between sites (see below) and phenotypes; the change of ϕ_{pot} was more important in large, closed canopy phenotypes (END & TN).

< **Figure 3** >

Environmental effects

The overall parameter effects on yield were only marginally higher at ROTH than ABER (0.73 and 0.81 Mg ha^{-1} ; Figure 3), but model sensitivity was higher in R2 than R1, which reflected the wetter growth conditions in R2, whilst R1 was characterised by water stress aggravated by higher cumulative radiation (**Table 1**). The relative sensitivity to changes of physiological parameters (photosynthesis) was similar for both sites when tested for potential production (NWS; Table S4). The effects of water stress reduced the overall sensitivity to changes of other physiological parameters (light interception and photosynthesis).

The SA revealed interactions between process and site, e.g. resulting in different parameter rankings related to temperature (budburst and senescence, μ_T) and water, both marginally more important at ROTH than ABER. The high ranking of WSP did not translate into similar differences caused by variation of water stress induced senescence, μ_{WS} (**Figure 2**). At ROTH the average effect of source related parameters on yield, like light interception (onset of branching, dl_{BioBr} , number of leaves per branch, NL_{Br} ; Ω ; η) and photosynthesis (ϕ and A_{max}) ranked lower than at ABER, which could reflect an interaction of light (lower radiation) and water availability. In contrast, parameters related to carbon allocation (sink size) ranked higher at ROTH than at ABER.

471 **Model calibration and cross-validation**

472 *Phenology, light interception and LUE*

473 Budburst parameter values showed a small variation among varieties (Table S3) with
 474 an average value of 6.1 ± 0.5 °C and -18.1 ± 0.4 for T_C and C_r , respectively. The
 475 model explained an overall 79% of the variance in budburst date at ABER. In 2013
 476 budburst showed a reduced goodness of fit by more than 10% at both sites as
 477 temperatures were outside the range of calibration.

478 Light interception is the result of a complex process of leaf area formation (eq. S2-
 479 4). Leaf area was first calibrated at ABER using only destructive LAI
 480 measurements, and then re-calibrated for water stress against the experimental
 481 evidence of LAI at ROTH during the first rotation (**Figure 4 C/F**).

482 <**Figure 4**>

483 The LAI simulation at ROTH (Endurance and Tora in **Figure 4A/F**, and Resolution
 484 and Terra Nova in **Figure S3**) was better during the first rotation than during the
 485 second (respective RMSE for Endurance were 0.95 and 1.78, Table 3). This was
 486 mainly due to delayed canopy development after coppicing in January 2012. Overall,
 487 the model reflected the genotypic differences between canopy types quite well but
 488 described LAI better for non-coppiced than coppiced years (RMSE of 0.76 and 1.26,
 489 respectively).

490 The parameters for photosynthesis were estimated against total biomass (e.g. **Figure**
 491 **4 D+E** + fine roots), and A_{max} in the range of 18.9 to 23.3 $\mu\text{mol m}^{-2} \text{s}^{-1}$ matched the
 492 sink demand well. For Terra Nova we calibrated a value similar to Endurance as
 493 both had a similar canopy. For comparison, photosynthesis was also expressed in
 494 terms of LUE, based on annual woody AGB (stem yield) and simulated intercepted
 495 PAR (**Figure 5A**) and averaged over all years (**Figure 5B**). LUE was 6% lower
 496 during 1st compared to 2nd rotation at ROTH but not at ABER. Overall, LUE at
 497 ROTH was lower than at ABER, mainly due to 2011, when Tora and Endurance
 498 suffered strong reductions (26 and 30%) due to drought.

499 <**Figure 5**>

500 *Sink formation – carbon allocation*

501 Potential stem elongation rates were initially calibrated using stem-height data
 502 during 2012 at ABER to avoid bias due to carbohydrate limitations and water stress.
 503 The parameter values for stem elongation (eq. S5) were then optimised through
 504 iteration using ABER genotype-specific growth data (time series) during the 1st
 505 rotation (2010-2011). These parameters fitted well the heights observed at ROTH
 506 (**Table 3**). The agreement between computed and observed stem extension rates is
 507 reflected in the stem growth dynamics at ROTH, in particular for the variety Tora
 508 (**Figure 4G**).

509 Stem number was strongly affected by the environment, with numbers significantly
 510 smaller at ABER than ROTH ($p < 0.01$) during 2010-2011, and genotype ($p < 0.001$)
 511 with Endurance having most and Resolution least. A significant interaction between
 512 sites and varieties ($p < 0.01$) was related to greater range in stem numbers among
 513 varieties at ROTH compared to ABER.

514 The relationship between stem height and diameter also showed a strong interaction
 515 between sites and varieties (Figure 5; $p < 0.001$). Data showed two separate groups,
 516 one for ROTH where stems are thinner and the other for ABER where stems are
 517 thicker, for an equivalent height. The parameters m_{DH} and c_{DH} were evaluated for
 518 each variety at each site from first rotation data (**Table S5**).

519 <Figure 6>

520 Destructive harvest data from both sites (first rotation) were used to approximate the
 521 partitioning between AGB and BGB in all varieties (e.g. Figure 4D, E; I, J; see also
 522 Figure S3 N,O; S,T). The four varieties allocated between 80% (Endurance) and
 523 90% (Resolution) of the dry matter to the AGB. Stem and stool biomass data at the
 524 end of rotations showed that all varieties allocated a smaller fraction of assimilates to
 525 BGB during R2 compared to R1. For Endurance it dropped from 20 to 15%, whilst
 526 Tora reduced allocation from 15.4 to 11.3%.

527 **Model Validation**

528 *Validation using the variety trial at ROTH*

529 The model validation was firstly done by comparing the average LAI, stem height
 530 and number, and AGB/ BGB yields measured in the second rotation of growth (R2)

at the dedicated variety trial at ROTH with the corresponding simulations (Table 3). The model predicted the differences in LAI between varieties well, with values for Endurance being highest and lowest for Tora (**Figure 4**). However, LAI modelling efficiency was low due to a phase shift of re-growth during the first year of the second rotation. Separating coppicing from non-coppicing years improved the statistical indicators of the prediction of LAI data (RMSE = 0.76; MD = -0.23; R^2 = 0.61).

<Table 3>

A management \times site effect was observed in terms of different stem numbers, height/diameter ratio between ABER versus ROTH across all four varieties (Fig 5). These observations suggested site-specific parameter values for A/BGB partitioning and initial stem numbers and height/thickness m_{DH} .

The final yield predictions agreed in a satisfactory way with the empirical data at ROTH for all four willow varieties for both rotations (R1, cross-validation; and R2, validation) (**Figure 6**). This result is consistent with the fact that for all the varieties we observed a high model efficiency and r^2 (>0.85 , Table 3) for stem biomass. The daily simulations for LAI, stem height and biomass, as well as stem number were within the 95% confidence interval of mean observations of these variables (**Figure 4**). The model was able to catch the behaviour of the studied traits throughout the growing seasons for all studied willow varieties. The comparison between measured and simulated BGB was satisfactory for most varieties (Figure 4E/J). ME was high for canopy height (all >0.9) and stem biomass yield (overall due to small number of samples ~ 0.99), and acceptable for BGB (overall ~ 0.28) whilst it was low for LAI and stem number (**Table 3**), due to slight asynchronies (**Figure 4**).

<Figure 7>

It is interesting to observe that in wet years [2012 (**Table S2**)] broadleaved varieties (e.g. Endurance, Figure 4D) performed better than the others (e.g. Tora, **Figure 4I**) but were more sensitive to water stress in 2010. The narrow leaf variety Resolution performed well in both rotations, irrespective of water stress (**Figure S3**), displaying an overall interesting $G \times E$ interaction. During the second rotation final yields in all varieties were significantly lower at ABER than ROTH. However, ABER second

rotation data could not be used for validation as the crop suffered exceptional wind damage that the model could not account for. Significant differences between genotypes ($p < 0.001$) established Endurance as the best yielder in both locations.

Validation with further yield data

Simulated and measured final biomass yields for three varieties compared well at ROTH and LARS (**Figure 8**). The overall correlation between measured and simulated biomass yields across both locations was good ($r^2 = 0.80$) and the average difference small and ME high ($MD = 0.68 \text{ Mg ha}^{-1}$; $ME = 0.7$). Most of the predictions concentrated near the 1:1-line, proving that the model was able to reproduce actual yields. It showed a slight bias toward lower yields at LARS and overestimated yields at ROTH.

<**Figure 8**>

Discussion

The process-based model LUCASS characterized phenotypic carbon sinks and implemented a sink-source interaction to describe yield formation for different SRC-willow genotypes. The novelty of this approach lies in its simplicity to parameterize the size of various sinks using phenotype-specific morphological characteristics. Calibrated and validated with data from sites across the UK, the model was able to illustrate the underlying system behavior in terms of source and sink dynamics and predicted final yields reflecting genotypic and environmental differences.

Key productivity parameters

Compared to other models (Amichev *et al.*, 2011; Deckmyn *et al.*, 2008; Tallis *et al.*, 2013) LUCASS has fewer parameters and less than 20 proved to be crucial for yield formation (**Figure 2**). The sensitivity analysis identified the onset of stem elongation, stem elongation rate and diameter as key parameters for yield formation and indicators of vigor (Kauter *et al.*, 2003; Volk *et al.*, 2006). Parameters of early development, e.g. chilling and forcing functions (Cesaraccio *et al.*, 2004; Fu *et al.*, 2013) were confirmed to be important at sites with a mild winter climate (ABER, LARS). Despite the importance of the start of spring growth (Cannell and Smith, 1983; Weih, 2009), it is not entirely clear whether chilling has a physiological role

(Horvath *et al.*, 2003; Rohde and Bhalerao, 2007) in addition to cold hardiness (Morin *et al.*, 2007). Further investigation is needed to determine whether chilling should be modelled for temperate tree species (Fu *et al.*, 2012). The role of photoperiod (Fu *et al.*, 2012) needs testing over a range of latitudes as sites studied here were similar. Nevertheless, this study did show that photoperiod was important for canopy development in terms of branching (dl_{BioBr}) and stem elongation (dl_{0SER}).

This analysis also showed that early budburst does not necessarily mean faster canopy development. Despite initial delays after coppicing, e.g. 2012, modelled and observed LAI reached their maxima at similar time and values, and the disparity had no impact on biomass production. A late spring start was apparently compensated for by faster leaf growth when environmental conditions became favorable (Weih, 2009). Thus, although budburst date is important for modelling willow development (Savage and Cavender-Bares, 2011), it remains debatable whether its accuracy is also important for predicting yield (Tallis *et al.*, 2013).

Genotypic differences for routes to high yields?

Source formation:

The variation of willow yield proved highly sensitive to parameters of LAI distribution and genotypic canopy characteristics, confirming that stem dynamics and biomass yield are strongly influenced by radiation distribution within the canopy (Bullard *et al.*, 2002a; Cerasuolo *et al.*, 2013; Ceulemans *et al.*, 1996; Tharakan *et al.*, 2008). Photosynthesis parameters (A_{max} , ϕ_{pot}) differed across genotypes (Andralojc *et al.*, 2014; Bonneau, 2004) and were also confirmed as an important source of yield variation (**Figures 2 and 3**). Quantum efficiency, ϕ_{pot} , consistently caused a larger model response than A_{max} , however, both seem to be strongly related, as found by (Andralojc *et al.*, 2014; Kaipiainen, 2009). Genotype ranking, according to photosynthetic capacity at the plant level, was dominated by leaf area but genotypes realized similar biomass with different strategies, either through high photosynthetic rate or large leaf area, confirming previous results (Andralojc *et al.*, 2014).

LUE is a key physiological indicator, usually expressed in terms of woody AGB per

unit absorbed PAR, which ranged from $0.6 \text{ g m}^{-2} \text{ MJ}^{-1}$ to $1.7 \text{ g m}^{-2} \text{ MJ}^{-1}$ (**Figure 6A**). Mean LUE was significantly higher at ABER (**Figure 6B**) indicating its interaction with drought and senescence (Savage *et al.*, 2009), canopy duration and leaf abscission (Weih, 2009) which can affect cumulative photosynthesis (Philippot, 1996). These site-specific differences due to water stress varied between broad- and narrow leaved varieties (Endurance and Tora, respectively). Tora evaded drought by means of a smaller leaf number (Cerasuolo *et al.*, 2013) and LAI (**Figure 4F**). The lowest LUE values were calculated for the first year of regrowth after establishment (2010), which was aggravated by drought at ROTH, especially for Endurance with its large canopy (-41%). *In situ* measurements under controlled water supply showed a similar drop in photosynthetic efficiency (-33 to -60%; (Bonneau, 2004)). The range of average LUE (0.77 to 1.47 g MJ^{-1}) which was significantly different between sites ($p < 0.01$) and varieties ($p < 0.001$) agreed with the range of simulated values (Jing *et al.*, 2012) and other estimates (Bullard *et al.*, 2002a; Sannervik *et al.*, 2006; Tallis *et al.*, 2013). A large canopy increased a variety's sensitivity to water stress, e.g. lowest LUE of Endurance irrespective of location, but achieved high yields in wet conditions. The effects of senescence on nutrient remobilization (Fracheboud *et al.*, 2009) and dry matter loss through respiration (de Neergaard *et al.*, 2002) can complicate the $G \times E$ interaction under variable climate.

Sink formation

Morphological characteristics were most important to identify high yielding genotypes especially under water stress conditions. The high sensitivity of these sink parameters across both sites (**Figure 2 and 3**) confirmed their importance for yield formation (Larsson, 1998). Traits, like stem number, height and diameter as well as leaf size and form, are also easily measured in high-throughput screening (Bullard *et al.*, 2002b; Martin and Stephens, 2006; Sannervik *et al.*, 2006; Sennerby-Forsse and Zsuffa, 1995; Verwijst *et al.*, 2012).

Our results confirmed earlier findings that Endurance had the thickest stems whilst Resolution the thinnest (Cunniff *et al.*, 2011). The genotype-specific relationship between stem diameter and height (**Figure 5**) is an excellent example of integrating plant characteristics and environment influence ($G \times E$ interaction). Stem diameter increases with length of coppicing cycle and is an important determinant for wood

654 quality (bark fraction) (Guidi *et al.*, 2009; Kauter *et al.*, 2003) and harvestable wood
655 volume (Amichev *et al.*, 2011; Bullard *et al.*, 2002b).

656 Moreover, parameter values for the potential allocated AGB were considered ~10-
657 12% lower than those estimated from destructive measurements. This was due to the
658 concurrence of two factors: around 30-40% of the NPP produced by basket willow
659 was used belowground, in particular on fine roots due to their high turnover rate
660 (Rytter, 2001). Experimental evidence provided by soil cores collected at ROTH
661 showed that actual fine root biomass was three times that from destructive samples,
662 e.g. Endurance 873 versus 283 g/m³, respectively (Cunniff *et al.*, 2015). These root
663 cores also showed that willows had a 65% greater fine root volume when grown at
664 ABER compared to ROTH.

665 The analysis of the experiments showed differences in carbon storage in BGB
666 (Cunniff *et al.*, 2015), which could have affected the regrowth dynamics (Sennerby-
667 Forsse and Zsuffa, 1995; Tharakan *et al.*, 2008; Verwijst *et al.*, 2012). Poor yields of
668 Tora under drought were shown to be concurrent with low initial BGB. Root
669 biomass could be a key trait to mitigate such circumstances (Ceulemans *et al.*, 1996).
670 Tora showed great resilience to yield high in the second growth cycle by building up
671 comparable fine root mass (Cunniff *et al.*, 2015). However, the G × E interaction is
672 not conclusive: in spite of more investment of carbon in BGB at ABER the vigour
673 after coppicing in 2012 dropped considerably (Cunniff *et al.*, 2015). Experimental
674 data also showed significant differences in biomass allocation among varieties
675 ($p < 0.001$) and in the interaction between site and variety ($p < 0.05$) (Cunniff *et al.*,
676 2015; Cunniff *et al.*, 2011). Stem numbers were possibly related to soluble
677 sugars/starch availability; but difficult to separate from management effects (cut-
678 back) at ABER which resulted in a smaller stool volume with fewer buds to develop
679 into new stems (Cunniff *et al.*, 2014).

680 Further analyses of the underlying physiological processes are needed to justify
681 different modelling approaches for early development (Fu *et al.*, 2012) and impact
682 on early growth (Tharakan *et al.*, 2008; Verwijst *et al.*, 2012) and yield formation. A
683 systematic budburst delay after coppicing can be expected (Verwijst *et al.*, 2012).
684 Bud and stem numbers could be influenced by stool size (management effect) as
685 well as starch and sugar contents (Cunniff *et al.*, 2014; Tschaplinski and Blake,

1995). This and evidence in regard to regrowth after coppicing (Tschaplinski and Blake, 1994; Von Fircks and Sennerby-Forsse, 1998) suggests model expansion to describe number of buds bursting as a function of readily available carbohydrate.

BGB characterization within the system is essential (Karp and Shield, 2008) but few data exist for roots of SRC (Agostini *et al.*, 2015; Cunniff *et al.*, 2015; Pacaldo *et al.*, 2013; Rytter, 2001). Destructive harvests represented only part of the belowground allocation (20 and 10% of the total measured biomass). A similar amount of fine root mass in a 1-m profile (3.56 and 6.46 Mg ha⁻¹) can be added (Cunniff *et al.*, 2015), which usually turns over fast (Rytter, 2001).

Source –sink interactions under different environments

Within the sink-source interaction the LAI and stem growth play the key roles for potential production, balancing the available CHO for resource capture and harvestable biomass. A hierarchy of dry matter allocation to leaves over stems was needed to enable sufficient light capture. In the model LAI is influenced by budburst and base temperature for leaf growth, which usually precede the day length threshold for stem elongation. Sufficient allocation of CHO to leaves (and fine roots) was secured by considering a genotype-specific T_{base} for stem elongation in the range of 8 to 10°C independent of location. These experimentally founded values are much higher than those suggested for the variety Jorr (2 to 7.6 °C) (Martin and Stephens, 2008). The discrepancy between T_{base} values for shoot extension is probably due to a different interpretation of this parameter. In contrast to T_{base} within a linear function of stem elongation rate and air temperature (Martin and Stephens, 2008) LUCASS used T_{base} to switch carbon allocation from “leaves only” to “leaves + stems”, stem elongation mainly depending on day length.

LAI between 2 and 4 were sufficient to reach high biomass yield (Jing *et al.*, 2012), suggesting that with the exception of Endurance, all varieties were source limited during the first year of regrowth (**Figure 4 and S3**). As LUCASS simulated seasonal dynamics of CHO reserves explicitly reserve pools balanced seasonal fluctuations in carbon availability. Overall, the agreement between measured and modelled sink indicators was good across the validation datasets (**Table 3**), even for stem numbers, although the dynamic of stem numbers was less well represented (**Figure 4**).

717 According to our simulations the stem as the major sink accounted for 75 to 97% of
718 the yield variance, variation of stool weights (**Figure 4**; 47 to 95%), and plausible
719 values for root dry matter. Furthermore, 94 and 80% of the yield variance was
720 captured across cross-validation at ROTH and independent data sets (LARS,
721 ROTH), respectively.

722 The necessity to define site specific initial bud and stem numbers to compensate for
723 environmental and management (coppicing) effects shows the need for a more
724 mechanistic description of coppicing response. Stored carbohydrates in the reserve
725 pools are essential for the initial growth of perennials (Philippot, 1996), and the
726 available evidence (Cunniff *et al.*, 2015; Cunniff *et al.*, 2014) would allow
727 implementation of a functional relationship between reserve availability and
728 stem/bud numbers to describe regrowth (Bullard *et al.*, 2002b; Tharakan *et al.*,
729 2008).

730 Allocation to BGB was a limiting factor for development of AGB during crop
731 establishment and can be considered as one cause for low yield during the first
732 rotation. Water limitation caused further significant reduction of AGB in favour of
733 BGB at ROTH, and LUCASS simulated both limitations adequately. The varieties
734 showed different responses towards water stress from a very sensitive Endurance to
735 an almost tolerant Resolution (Bonneau, 2004; Larsen *et al.*, 2014; Savage and
736 Cavender-Bares, 2011). New evidence from specific experiments with potential-
737 and limited-water treatments will follow in future.

738 In conclusion, this model represents a valuable research tool to improve selection
739 and breeding programs for site-specific SRC crops in support of the “fuel versus
740 food” debate and to explore climate and land use scenarios for the development of
741 biomass resources needed for the bioeconomy. LUCASS’ ability to simulate
742 allocation to BGB also allows improvement of the terrestrial carbon balance and soil
743 carbon sequestration to be assessed.

744

745 **Supplementary data**

746 *Model equations S1 to S7*

747 *Supplementary Figures*

748 Figure S1: Global solar radiation (- -), air temperature (—) and precipitation
749 (filled bar) at Rothamsted (a) and Aberystwyth (b) during the experiment (2010-13)

750 Figure S2: Heat map from sensitivity analysis displaying the average
751 response strength (μ) estimated using the Morris' method, run for all varieties at both
752 sites, Harpenden (ROTH) and Aberystwyth (ABER) with weather data for first (R1,
753 2010-11) and second rotation (R2, 2012-13). Simulations were done in absence of
754 water stress (NWS) and under actual water stress (WS).

755 Figure S3: Observed (filled circles) and simulated (solid line) leaf area index
756 (LAI), canopy height, stem number and accumulated stem (AGB) and stool (BGB)
757 biomass of Resolution (K-O) and Terra Nova (P-T) grown at Rothamsted over two
758 consecutive 2-year rotations (2010-11; 2012-13). The error bars represent the
759 standard deviations of the experimental values (n=4)

760 *Supplementary Tables*

761 Table S1: Physical characteristics of the soil in three sites using Soil
762 Classification System for England and Wales: Harpenden (ROTH), Aberystwyth
763 (ABER) and Long Ashton Research Station (LARS); soil depth, bulk density, soil
764 texture (sand, silt and clay), soil organic carbon (SOC), volumetric water content at
765 field capacity θ_{fc} and permanent wilting point θ_{pwp} , available water capacity (AWC)
766 in the profile derived using the Hypres pedotransfer function (Wösten *et al.*, 1999).

767 Table S2 Cumulative annual precipitation, radiation, and average minimum
768 and maximum temperature (2010-2013) and the two sites (ROTH and ABER)

769 Table S3: Optimised values of the parameters T_C and C_r of the chilling model
770 (1) for each willow variety.

771 Table S4: Results of the sensitivity analysis for ROTH and ABER simulated
772 under potential (NWS) and water-limited (WS) production for (a) the first (2010-11)
773 and (b) the second coppice rotation (2012-13).

774 Table S5: Parameter values for the stem height/diameter relationship, for the
775 four studied varieties (Endurance, Resolution, Terra Nova and Tora) and the two
776 dedicated trials (ROTH and ABER).

777 **Acknowledgments**

778 The authors would like to thank the Biotechnological and Biological Sciences
779 Research Council (BBSRC) and Ceres Inc. for funding this work within the
780 “BBSRC Sustainable Bioenergy Centre (BSBEC): Perennial Bioenergy Crops
781 Programme” (BB/G016216/1; <http://www.bsbec-biomass.org.uk/>). We would also like
782 to thank Tim Barraclough, March Castle, William Macalpine and Peter Fruen
783 (Rothamsted), and Anne Maddison and Laurence Jones (Aberystwyth) for their
784 dedicated work collecting data in the field.

785

786 **Tables**

787 Table 1: Meteorological indicators during dormancy (November – March) and growth (April
 788 – October) periods mean maximal and minimal air temperature (T_{\max} , T_{\min}) and
 789 cumulative annual global radiation (R_g) and precipitation (P).

Site	Dormancy		Growth		R_g (MJ m ⁻²)	P (mm)
	T_{\max}	T_{\min}	T_{\max}	T_{\min}		
	(°C)					
ROTH	7.6	1.8	17.7	9.0	3910	680
ABER	9.0	3.8	16.6	11.6	3560	1020
LARS	9.2	3.1	18.5	10.4	3740	760

790

791

792

Table 2: Alphabetical list according to process of model parameters used in LUCASS;
symbols, definition and units as well as source (reference, experimental evidence)

Symbol	Definition	Units	Reference/Comments
Phenology			
C_r	Chilling requirement	d	Optimised
d_{ac}	Number of day necessary to the crop to reallocate resources	d	Optimised
dd_{fill}	GDD for max stem filling rate	°C d	Calibrated
dl_{OSER}	Stem elongation rate, intersect	d	Measured
dl_{BtoBr}	Base photoperiod of buds becoming branches	d d ⁻¹	Assumed
$dl_{maxBtoBr}$	Photoperiod for maximum rate of buds becoming branches	d d ⁻¹	Assumed
$NBuds_0$	Initial bud number	-	Measured
T_B	Base temperature for above ground growth	°C	(Perttu and Philippot, 1996)
T_c	half-efficiency temperature	°C	Optimised
$T_{optBtoBr}$	Optimum temperature for buds becoming branches	°C	Calibrated
Morphology – Sink Formation			
a_{Stl}	Linear coefficient in the stool elongation rate	mm d ⁻¹	Calibrated
$a_{Stl/H}$	Linear coefficient in the linear relationship Stem height-Stool weight	m g ⁻¹	Calibrated
b_{Rt}	Root elongation rate	m d ⁻¹ °C ⁻¹	Calibrated
b_{Stl}	Constant coefficient in the stool elongation rate	mm d ⁻¹ °C ⁻¹	Calibrated
$b_{Stl/H}$	Constant coefficient in the linear relationship Stem height-Stool weight	m	Calibrated
C_{BtoBr}	Maximum relative rate of buds producing branches	d ⁻¹	Calibrated
C_{LER}	Leaf extension, constant	m	(Porter <i>et al.</i> , 1993)
f_{fill}	Power for stem filling rate	-	Calibrated
$ff_{maxBtoBr}$	Maximum proportion of buds that produce new branches	-	Calibrated
h_{0DH}	Relationship diameter/height intersect	mm	Measured
LAI_{CShade}	Minimum LAI for shading to cause senescence	m ² m ⁻²	Calibrated
l_{distr}	Leaf layers distribution	-	(Cerasuolo <i>et al.</i> , 2013)
L_{fShp}	Leaf shape factor	-	Measured
L_{fWith}	Leaf width	m	Measured
ls_{Br}	Relative reduction of branching with increased LAI	-	Calibrated
m_{DH}	Relationship diameter/height slope	mm m ⁻¹	Measured
m_{LER}	Leaf elongation linear coefficient	m d ⁻¹	(Porter <i>et al.</i> , 1993)
m_{SER}	Stem elongation rate, slope	m d ⁻¹	Measured
NL_{Br}	Number of leaves per branch	-	Calibrated
n_{Stlwt}	Power coefficient for the estimation of the stool weight factor	-	Calibrated
$n_{maxStlwt}$	Stool weight at which the stool weight factor reaches its maximum effect	g m ⁻²	Calibrated
ρ_{AG}	Fraction of assimilates going to the above-ground organs	-	Measured
ρ_{Rt}	Fraction of below-ground assimilates going to roots	-	Measured
ρ_{St}	Specific stem weight	g m ⁻²	Measured
SLA_{max}	Maximum specific leaf area	m ² g ⁻¹	Measured
SLA_{min}	Minimum specific leaf area	m ² g ⁻¹	Measured
St_{max}	Max stem number given the initial number of buds	-	Calibrated

η_{St}	Stems shape parameter	-	Assumed
Symbol	Definition	Units	Reference/Source
Cont'd Morphology – Sink Formation			
μ_{Br}	Porter mortality factor - lower asymptote	-	(Porter <i>et al.</i> , 1993)
μ_W	Branches and stems aging death rate	d ⁻¹	Measured
μ_{WRes}	Percentage of woody reserves lost during the harvest	g g ⁻¹	Calibrated
σ_{Rt}	Root dry matter per unit length	g m ⁻¹	Calibrated
σ_{Stl}	Stool structural dry matter per unit length	g m ⁻¹	Calibrated
W_{loss}	Percentage of dry matter lost during the harvest	-	Calibrated
Physiology – Source Formation			
<i>Light Interception</i>			
α	ELADP quadratic coefficient	-	Observed
β	ELADP linear coefficient	-	Observed
γ	ELADP constant	-	Observed
η	Shape parameter for the vertical leaf area distribution	-	(Cerasuolo <i>et al.</i> , 2013)
Ω	Clumping index	-	Cerasuolo et al. (2013)
μ_T	Temperature-driven increase of senescence	d ⁻¹	
$\mu_{maxShade}$	Maximum shading-induced senescence rate	d ⁻¹	Calibrated
μ_{Shade}	Shading-induced increase of senescence rate per unit of LAI	d ⁻¹	Calibrated
μ_{WS}	Water stress-driven increase of senescence	d ⁻¹	Calibrated
<i>Assimilation and respiration</i>			
A_{max}	CO ₂ potential assimilation rate at light saturation	g(CO ₂) m ⁻² s ⁻¹	(Bonneau, 2004)
P_{cmax}	Max photosynthetic rate capacity	μg(CO ₂) m ⁻² s ⁻¹	(Bonneau, 2004)
p_{Lf}	Percentage of single leaves produced by new flushing buds	-	Calibrated
Q_{10}	Responsiveness of respiration at a temperature of 10°C	-	(Sampson and Ceulemans, 2000)
r_b	Boundary layer resistance	s m ⁻¹	Calibrated
R_{BG}	Maintenance respiration rate of roots	g(glucose) d ⁻¹	(Vivin <i>et al.</i> , 2002)
R_D	Dark respiration	μg(CO ₂) m ⁻² s ⁻¹	(Kaipainen, 2009)
ReS_{max}	Maximum Reserve Fraction	-	Calibrated
ReS_{maxStl}	Maximum reserve fraction of stool DM	-	Calibrated
R_{Lf}	Maintenance respiration rate of leaves	g(glucose) d ⁻¹	Vivin et al. (2002)
$r_{s,min}$	Minimum stomatal resistance	s m ⁻¹	Bonneau (2004)
R_{St}	Maintenance respiration rate of stems	g(glucose) d ⁻¹	Vivin et al. (2002)
T_{bC}	Base temperature in CO ₂ assimilation	°C	Assumed
T_{BG}	Base temperature for below ground growth	°C	Assumed
T_{maxC}	Maximum temperature in CO ₂ assimilation	°C	(van Laar <i>et al.</i> , 1992)
T_{minC}	Minimum temperature in CO ₂ assimilation	°C	
T_{optC}	Optimal temperature in CO ₂ assimilation	°C	
WSP	Water stress parameter	-	Calibrated
Γ	CO ₂ compensation point at 25°C	μmol/mole	(Xu <i>et al.</i> , 2008)
ξ_{GW}	Conversion of assimilates to biomass	g(glucose) g ⁻¹	(Penning de Vries <i>et al.</i> , 1983)
ϕ_{pot}	Quantum efficiency of photosynthesis	μg CO ₂ J ⁻¹	Bonneau (2004)
σ	Scattering coefficient of leaves for PAR	-	(Goudriaan, 1988)

Table 3: Goodness of fit for modelling growth indicators (LAI, canopy height h_c ; number of stems n_{stems} ; biomass of stem B_{stem} and stool B_{stool}) and overall yield of four willow varieties grown at Rothamsted for the first (R1, 2010-2011) and second (R2, 2012-2013) rotation used for validation; Residual Mean Square Error (RMSE), Mean Difference (MD), modelling efficiency (ME) and certainty (R^2)

Variety	Indicator	RMSE		MD (O-S)		ME		R^2	
		R1	R2	R1	R2	R1	R2	R1	R2
Endurance	LAI [$\text{m}^2 \text{m}^{-2}$]	0.95	1.78	-0.09	-1.24	0.07	-0.45	0.25	0.38
	h_c [m]	0.30	0.26	-0.18	-0.08	0.89	0.96	0.95	0.97
	n_{stems} [m^{-2}]	6.39	7.24	4.40	2.97	0.02	0.15	0.55	0.95
	B_{stem} [Mg ha^{-1}]	1.98	0.87	1.49	0.39	0.90	0.99	0.96	1.00
	B_{stool} [Mg ha^{-1}]	1.37	2.38	0.85	1.74	-0.03	-0.06	0.62	0.58
Resolution	LAI [$\text{m}^2 \text{m}^{-2}$]	0.70	0.93	0.45	-0.40	-2.67	-0.23	0.03	0.37
	h_c [m]	0.29	0.32	0.16	-0.18	0.94	0.94	0.96	0.96
	n_{stems} [m^{-2}]	6.64	4.04	3.92	2.04	-0.18	-0.15	0.78	0.66
	B_{stem} [Mg ha^{-1}]	1.86	1.20	0.39	-0.91	0.89	0.99	0.90	1.00
	B_{stool} [Mg ha^{-1}]	0.80	1.57	0.53	1.19	-0.10	-0.01	0.84	0.95
Terra Nova	LAI [$\text{m}^2 \text{m}^{-2}$]	0.79	1.17	0.35	-0.63	-0.96	-1.07	0.03	0.35
	h_c [m]	0.23	0.31	0.14	0.16	0.94	0.93	0.96	0.96
	n_{stems} [m^{-2}]	3.87	2.58	-0.19	1.18	0.30	0.11	0.74	0.46
	B_{stem} [Mg ha^{-1}]	1.73	0.99	-0.36	0.22	0.91	0.99	0.95	0.99
	B_{stool} [Mg ha^{-1}]	1.02	1.30	-0.74	-1.29	-0.02	-0.06	0.94	1.00
Tora	LAI [$\text{m}^2 \text{m}^{-2}$]	0.45	1.17	0.10	-0.61	-0.63	-1.54	0.15	0.28
	h_c [m]	0.16	0.21	-0.03	0.03	0.97	0.98	0.98	0.98
	n_{stems} [m^{-2}]	2.28	5.15	0.43	4.21	0.44	-1.45	0.76	0.76
	B_{stem} [Mg ha^{-1}]	1.69	0.11	0.04	0.11	0.85	1.00	0.95	1.00
	B_{stool} [Mg ha^{-1}]	0.64	0.96	-0.52	0.49	-0.33	0.56	0.91	0.91
All*	B_{stem} [Mg ha^{-1}]	1.81	0.89	0.38	-0.05	0.90	0.99	0.92	0.99
	B_{stool} [Mg ha^{-1}]	1.00	1.64	0.06	0.53	0.22	0.28	0.26	0.41

*Due to a small number of observations during R2 for biomass ($n = 3$ compared to >10 for the other indicators), the data were pooled together to have an overall estimation.

Figure captions

Figure 1: Flowchart of the process-based willow growth model, LUCASS, embedded into a water and energy balance framework

Figure 2: Heat map for the average of response strength (μ) estimated using the Morris' method and ranking calculated for all varieties together or separated according to potential and water-limited conditions (All WS&NWS, All NWS, All WS). Average sensitivity was calculated under water-limited conditions for first (WS R1), second rotation (WS R2) separately, for sites considering both rotations (ABER WS R1+R2, ROTH WS R1+R2), and across similar canopy phenotypes (Endurance and Terra Nova – END & TN; Resolution and Tora – RES & T). – Colour intensity increases with increasing response strength but is lower for higher ranks

Figure 3: Morris sensitivity measures (μ^* , σ) under water-limited production to random changes of 34 model parameters averaged across all genotypes for Rothamsted (A, C) and Aberystwyth (B, D) during first and second rotation, respectively. Symbols represent pheno- (▪), morpho- (◻) logical sink-related parameters, physiological (•) and other source-related parameters (°)

Figure 4: Observed (filled circles) and simulated (solid line) leaf area index (LAI), canopy height, stem number and accumulated stem (AGB) and stool (BGB) yield of Endurance (A-E) and Tora (F-J) grown at Rothamsted over two consecutive rotations (2010-11; 2012-13). The error bars represent the standard deviations of the experimental values (n=4)

Figure 5: Light use efficiency (LUE, g AGB MJ⁻¹ APAR) (A) during the time course of the experiment (2010-2013) for the varieties Tora (◻ ■) and Endurance (Δ ▲) at ROTH (open) and ABER (closed) and (B) averaged for all varieties at both sites

Figure 6: Correlations between stem diameter and stem height for Endurance at (A) ROTH and (B) ABER and (C) sketched for all willow varieties (Endurance —, Resolution - - -, Terra Nova — · —, Tora ·····) for ROTH (bold) and ABER (fine)

Figure 7: Observed (black) and simulated (white) accumulated yields of four willow varieties (A) for calibration during 1st coppice cycle (2010-2011) at ABER and (B) validation over two 2-year coppice cycles 2010-2011 (a) and 2012-2014 (b) at ROTH

Figure 8: Correlation between measured vs simulated biomass yield of three willow varieties from trials at ROTH (closed symbols) and LARS (open symbols). Endurance : ◻ ■, Resolution : Δ ▲, Tora: ○ ●

References

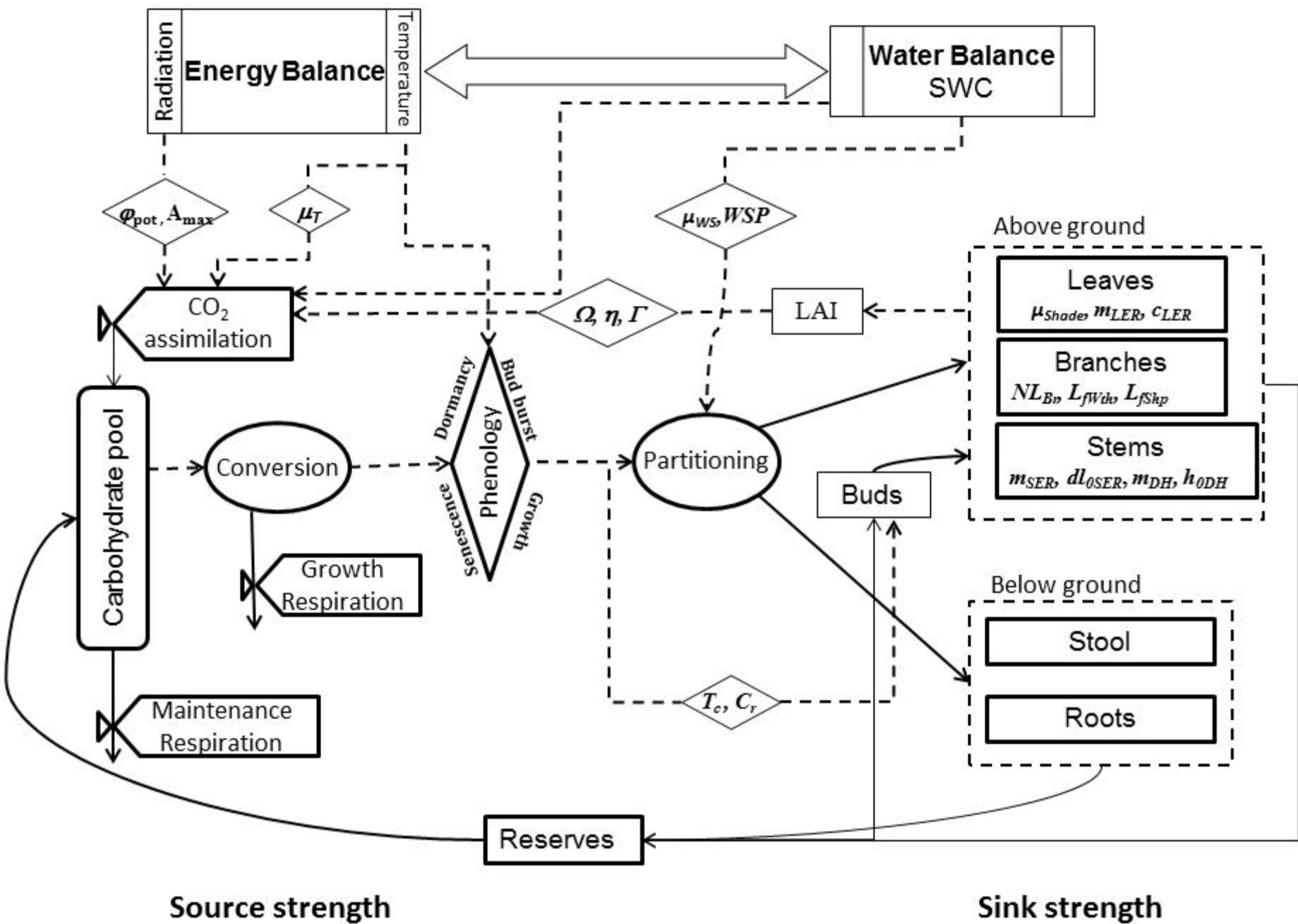
- Agostini F, Gregory AS, Richter GM.** 2015. Carbon sequestration under perennial energy crops: is the jury still out? *BioEnergy Research* **8**, 000-000.
- Amichev BY, Hangs RD, Van Rees KCJ.** 2011. A novel approach to simulate growth of multi-stem willow in bioenergy production systems with a simple process-based model (3PG). *Biomass and Bioenergy* **35**, 473-488.
- Andralojc PJ, Bencze S, Madgwick PJ, Philippe H, Powers SJ, Shield I, Karp A, Parry MAJ.** 2014. Photosynthesis and growth in diverse willow genotypes. *Food and Energy Security* **3**, 69-85.
- Aylott MJ, Casella E, Tubby I, Street NR, Smith P, Taylor G.** 2008. Yield and spatial supply of bioenergy poplar and willow short-rotation coppice in the UK. *New Phytologist* **178**, 358-370.
- Bonneau LJG.** 2004. Drought resistance of willow short rotation coppice genotypes. Doctor of Philosophy, Cranfield, Silsoe, 211 + VII.
- Bullard MJ, Mustill SJ, Carver P, Nixon PMI.** 2002a. Yield improvements through modification of planting density and harvest frequency in short rotation coppice *Salix* spp. - 2. Resource capture and used in two morphologically diverse varieties. *Biomass & Bioenergy* **22**, 27-39.
- Bullard MJ, Mustill SJ, McMillan SD, Nixon PMI, Carver P, Britt CP.** 2002b. Yield improvements through modification of planting density and harvest frequency in short rotation coppice *Salix* spp. - 1. Yield response in two morphologically diverse varieties. *Biomass & Bioenergy* **22**, 15-25.
- Cannell MGR, Smith RI.** 1983. THERMAL TIME, CHILL DAYS AND PREDICTION OF BUDBURST IN *PICEA-SITCHENSIS*. *Journal of Applied Ecology* **20**, 951-963.
- Cerasuolo M, Richter GM, Cunniff J, Purdy S, Shield I, Karp A.** 2013. A pseudo-3D model to optimise the target traits of light interception in short-rotation coppice willow. *Agricultural and Forest Meteorology* **173**, 127-138.
- Cesaraccio C, Spano D, Snyder RL, Duce P.** 2004. Chilling and forcing model to predict bud-burst of crop and forest species. *Agricultural and Forest Meteorology* **126**, 1-13.
- Ceulemans R, McDonald AJS, Pereira JS.** 1996. A comparison among eucalypt, poplar and willow characteristics with particular reference to a coppice, growth-modelling approach. *Biomass & Bioenergy* **11**, 215-231.
- Chuine I.** 2000. A unified model for budburst of trees. *Journal of Theoretical Biology* **207**, 337-347.
- Cunniff J, Purdy SJ, Barraclough T, Castle M, Maddison AL, Jones LE, Shield IF, Gregory AS, Karp A.** 2015. High yielding biomass ideotypes of willow (*Salix* spp.) show differences in below ground biomass allocation. *Biomass & Bioenergy* **80**, 114-127.
- Cunniff J, Shield I, Barraclough T, Castle M, Hanley S, Andralojc J, Richter G, Cerasuolo M, Purdy S, Clifton-Brown J, Maddison A, Jones L, Donnison I, Karp A.** 2011. BSBEC-BioMASS - Selecting traits to optimise biomass yield of SRC willow. *Biomass and Energy Crops*, Vol. Aspects of Applied Biology, 83-91.
- Cunniff J, Shield I, Purdy S, Karp A.** 2014. Phenological dynamics of above and below ground biomass and non- structural carbohydrates in the perennial bioenergy crop willow. International Poplar Symposium.
- de Neergaard A, Porter JR, Gorissen A.** 2002. Distribution of assimilated carbon in plants and rhizosphere soil of basket willow (*Salix viminalis* L.). *Plant and Soil* **245**, 307-314.
- De Pury DGG, Farquhar GD.** 1997. Simple scaling of photosynthesis from leaves to canopies without the errors of big-leaf models. *Plant, Cell and Environment* **20**, 537-557.

- Deckmyn G, Laureysens I, Garcia J, Muys B, Ceulemans R.** 2004. Poplar growth and yield in short rotation coppice: model simulations using the process model SECRETS. *Biomass & Bioenergy* **26**, 221-227.
- Deckmyn G, Verbeeck H, de Beeck MO, Vansteenkiste D, Steppe K, Ceulemans R.** 2008. ANAFORE: A stand-scale process-based forest model that includes wood tissue development and labile carbon storage in trees. *Ecological Modelling* **215**, 345-368.
- Fourcaud T, Zhang X, Stokes A, Lambers H, Korner C.** 2008. Plant growth modelling and applications: The increasing importance of plant architecture in growth models. *Annals of Botany* **101**, 1053-1063.
- Fracheboud Y, Luquez V, Bjorken L, Sjodin A, Tuominen H, Jansson S.** 2009. The Control of Autumn Senescence in European Aspen. *Plant Physiology* **149**, 1982-1991.
- Fu YH, Campioli M, Deckmyn G, Janssens IA.** 2013. Sensitivity of leaf unfolding to experimental warming in three temperate tree species. *Agricultural and Forest Meteorology* **181**, 125-132.
- Fu YS, Campioli M, Van Oijen M, Deckmyn G, Janssens IA.** 2012. Bayesian comparison of six different temperature-based budburst models for four temperate tree species. *Ecological Modelling* **230**, 92-100.
- Genard M, Dauzat J, Franck N, Lescourret F, Moitrier N, Vaast P, Vercambre G.** 2008. Carbon allocation in fruit trees: from theory to modelling. *Trees-Structure and Function* **22**, 269-282.
- Goudriaan J.** 1988. The Bare Bones of Leaf-Angle Distribution in Radiation Models for Canopy Photosynthesis and Energy Exchange. *Agricultural and Forest Meteorology* **43**, 155-169.
- Goudriaan J, van Laar HH.** 1994. *Modelling Potential Crop Growth Processes. Textbook with Exercises.* Wageningen: Kluwer Academic Publishers.
- Guidi W, Tozzini C, Bonari E.** 2009. Estimation of chemical traits in poplar short-rotation coppice at stand level. *Biomass & Bioenergy* **33**, 1703-1709.
- Heilman PE, Ekuan G, Fogle D.** 1994. ABOVEGROUND AND BELOWGROUND BIOMASS AND FINE ROOTS OF 4-YEAR-OLD HYBRIDS OF POPULUS-TRICHOCARPA X POPULUS-DELTOIDES AND PARENTAL SPECIES IN SHORT-ROTATION CULTURE. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* **24**, 1186-1192.
- Hlaszny E, Hajdu E, Gy B, Ladanyi M.** 2012. COMPARISON OF BUDBURST MODELS PREDICTIONS FOR KEKFRANKOS. *Applied Ecology and Environmental Research* **10**, 75-86.
- Hoeglind M, Hanslin HM, Van Oijen M.** 2005. Timothy regrowth, tillering and leaf area dynamics following spring harvest at two growth stages. *Field Crops Research* **93**, 51-63.
- Horvath DP, Anderson JV, Chao WS, Foley ME.** 2003. Knowing when to grow: signals regulating bud dormancy. *Trends in Plant Science* **8**, 534-540.
- Jing Q, Conijn SJG, Jongschaap REE, Bindraban PS.** 2012. Modeling the productivity of energy crops in different agro-ecological environments. *Biomass and Bioenergy* **46**, 618-633.
- Kaipainen E.** 2009. Parameters of photosynthesis light curve in *Salix dasyclados* and their changes during the growth season. *Russian Journal of Plant Physiology* **56**, 445-453.
- Karp A, Hanley SJ, Trybush SO, Macalpine W, Pei M, Shield I.** 2011. Genetic Improvement of Willow for Bioenergy and Biofuels Free Access. *Journal of Integrative Plant Biology* **53**, 151-165.
- Karp A, Richter GM, Shield IF, Hanley SH.** 2014. Genetics, genomics and crop modelling: integrative approaches to the improvement of biomass willows. In: McCann MC, Buckeridge MS, Carpita NC, eds. *Plants and BioEnergy*, Vol. 4. New York: Springer Science+Business Media, 107-130.
- Karp A, Shield I.** 2008. Bioenergy from plants and the sustainable yield challenge. *New Phytologist* **179**, 15-32.

- Kauter D, Lewandowski I, Claupein W.** 2003. Quantity and quality of harvestable biomass from *Populus* short rotation coppice for solid fuel use--a review of the physiological basis and management influences. *Biomass and Bioenergy* **24**, 411-427.
- Larsen S, Jørgensen U, Lærke P.** 2014. Willow Yield Is Highly Dependent on Clone and Site. *BioEnergy Research* **7**, 1280-1292.
- Larsson S.** 1998. Genetic improvement of willow for short-rotation coppice. *Biomass and Bioenergy* **15**, 23-26.
- Laureysens I, Deraedt W, Indeherberge T, Ceulemans R.** 2003. Population dynamics in a 6-year old coppice culture of poplar. I. Clonal differences in stool mortality, shoot dynamics and shoot diameter distribution in relation to biomass production. *Biomass and Bioenergy* **24**, 81-95.
- Le Roux X, Lacoite A, Escobar-Gutierrez A, Le Dizes S.** 2001. Carbon-based models of individual tree growth: A critical appraisal. *Annals of Forest Science* **58**, 469-506.
- Martin PJ, Stephens W.** 2006. Willow growth in response to nutrients and moisture on a clay landfill cap soil. I. Growth and biomass production. *Bioresource Technology* **97**, 437-448.
- Martin PJ, Stephens W.** 2008. Willow water uptake and shoot extension growth in response to nutrient and moisture on a clay landfill cap soil. *Bioresource Technology* **99**, 5839-5850.
- Matthews RW.** 2001. Modelling of energy and carbon budgets of wood fuel coppice systems. *Biomass & Bioenergy* **21**, 1-19.
- Mcdonald AJS, Stadenberg I.** 1993. Diurnal Pattern of Leaf Extension in *Salix-Viminalis* Relates to the Difference in Leaf Turgor before and after Stress-Relaxation. *Tree Physiology* **13**, 311-318.
- Morin X, Ameglio T, Ahas R, Kurz-Besson C, Lanta V, Lebourgeois F, Miglietta F, Chuine I.** 2007. Variation in cold hardiness and carbohydrate concentration from dormancy induction to bud burst among provenances of three European oak species. *Tree Physiology* **27**, 817-825.
- Morris MD.** 1991. Factorial sampling plans for preliminary computational experiments. *Technometrics* **33**, 161-174.
- Pacaldo RS, Volk TA, Briggs RD.** 2013. Greenhouse Gas Potentials of Shrub Willow Biomass Crops Based on Below- and Aboveground Biomass Inventory Along a 19-Year Chronosequence. *BioEnergy Research* **6**, 252-262.
- Payne RW, Harding SA, Murray DA, Soutar DM, Baird DB, Glaser AI, Welham SJ, Gilmour AR, Thompson R, Webster R.** 2011. *The Guide to GenStat Release 14*. Hemel Hempstead, UK: VSN International.
- Penning de Vries FWT, Van Laar HH, Chardon MCM.** 1983. Bioenergetics of growth of seeds, fruits and storage organs. In: Smith WH, Banta SJ, eds. *Potential productivity of field crops under different environments*. Los Banos, Philippines:: IRRI, 37-59.
- Perttu KL, Philippot S.** 1996. Modelling short rotation forestry growth (Uppsala, Sweden, 24-26 October 1994). *Biomass & Bioenergy* **11**, 69-71.
- Philippot S.** 1996. Simulation models of short-rotation forestry production and coppice biology. *Biomass & Bioenergy* **11**, 85-93.
- Porter JR, Parfitt RI, Arnold GM.** 1993. Leaf Demography in Willow Short-Rotation Coppice. *Biomass & Bioenergy* **5**, 325-336.
- Powers SJ, Peacock L, Yap ML, Brain P.** 2006. Simulated beetle defoliation on willow genotypes in mixture and monotype plantations. *Annals of Applied Biology* **148**, 27-38.
- Pretzsch H, Grote R, Reineking B, Roetzer T, Seifert S.** 2008. Models for forest ecosystem management: A European perspective. *Annals of Botany* **101**, 1065-1087.
- Richter GM, Acutis M, Trevisiol P, Latiri K, Confalonieri R.** 2010. Sensitivity analysis for a complex crop model applied to Durum wheat in the Mediterranean. *European Journal of Agronomy* **32**, 127-136.
- Richter GM, Rana G, Ferrara RM, Ventrella D, Acutis M, Trevisiol P, Mayr T, Baggaley N, Morris J, Holmes A, Trawick P, Dailey AG, Robbins P, Simota C,**

- Whitmore AP, Powlson DS.** 2006. Stability and Mitigation of Arable Systems in Hilly Landscapes. *Final Report*. Brussels: European Commission, 280.
- Rinne PLH, Welling A, Vahala J, Ripel L, Ruonala R, Kangasjarvi J, van der Schoot C.** 2011. Chilling of Dormant Buds Hyperinduces FLOWERING LOCUS T and Recruits GA-Inducible 1,3-beta-Glucanases to Reopen Signal Conduits and Release Dormancy in Populus. *Plant Cell* **23**, 130-146.
- Robinson KM, Karp A, Taylor G.** 2004. Defining leaf traits linked to yield in short-rotation coppice Salix. *Biomass & Bioenergy* **26**, 417-431.
- Rohde A, Bhalerao RP.** 2007. Plant dormancy in the perennial context. *Trends in Plant Science* **12**, 217-223.
- Rytter RM.** 2001. Biomass production and allocation, including fine-root turnover, and annual N uptake in lysimeter-grown basket willows. *Forest Ecology and Management* **140**, 177-192.
- Sampson DA, Ceulemans R.** 2000. SECRETS: simulated carbon fluxes from a mixed coniferous/deciduous Belgian forest. In: Ceulemans R, Veroustraete F, Gond V, Van Rensbergen JBHF, eds. *Forest ecosystem modeling, upscaling and remote sensing*: SPB Academic Publishing bv, 95 -108.
- Sannervik AN, Eckersten H, Verwijst T, Kowalik P, Nordh N-E.** 2006. Simulation of willow productivity based on radiation use efficiency, shoot mortality and shoot age. *European Journal of Agronomy* **24**, 156-164.
- Savage JA, Cavender-Bares J, Verhoeven A.** 2009. Willow species (genus: Salix) with contrasting habitat affinities differ in their photoprotective responses to water stress. *Functional Plant Biology* **36**, 300-309.
- Savage JA, Cavender-Bares JM.** 2011. Contrasting drought survival strategies of sympatric willows (genus: Salix): consequences for coexistence and habitat specialization. *Tree Physiology* **31**, 604-614.
- Schapendonk AHCM, Stol W, van Kraalingen DWG, Bouman BAM.** 1998. LINGRA, a sink/source model to simulate grassland productivity in Europe. *European Journal of Agronomy* **9**, 87-100.
- Sennerby-Forsse L, Zsuffa L.** 1995. Bud structure and resprouting in coppiced stools of *Salix viminalis* L., *S. eriocephala* Michx., and *S. amygdaloides* Anders. *Trees - Structure and Function* **9**, 224-234.
- Sinclair TR.** 1986. Water and nitrogen limitations in soybean grain production. Part I. Model development. *Field Crops Res.* **15**, 125 – 141.
- Smith P, Smith JU, Powlson DS, McGill WB, Arah JRM, Chertov OG, Coleman K, Franko U, Frohling S, Jenkinson DS, Jensen LS, Kelly RH, Klein-Gunnewiek H, Komarov AS, Li C, Molina JAE, Mueller T, Parton WJ, Thornley JHM, Whitmore AP.** 1997. A comparison of the performance of nine soil organic matter models using datasets from seven long-term experiments. *Geoderma* **81**, 153-225.
- Stanton BJ, Serapiglia MJ, Smart LB.** 2014. The domestication and conservation of Populus and Salix genetic resources. In: Isebrands JG, Richardson J, eds. *Poplars and willows: trees for society and the environment*. Wallingford, UK: CAB International, 124-199.
- Tallis MJ, Casella E, Henshall PA, Aylott MJ, Randle TJ, Morison JIL, Taylor G.** 2013. Development and evaluation of ForestGrowth-SRC a process-based model for short rotation coppice yield and spatial supply reveals poplar uses water more efficiently than willow. *Global Change Biology Bioenergy* **5**, 53-66.
- Teixeira EI, Moot DJ, Brown HE, Pollock KM.** 2007. How does defoliation management impact on yield, canopy forming processes and light interception of lucerne (*Medicago sativa* L.) crops? *European Journal of Agronomy* **27**, 154-164.
- Tharakan PJ, Volk TA, Nowak CA, Ofezu GJ.** 2008. Assessment of Canopy Structure, Light Interception, and Light-use Efficiency of First Year Regrowth of Shrub Willow (*Salix* sp.). *BioEnergy Research* **1**, 229-238.

- Toillon J, Rollin B, Dalle E, Feinard-Duranceau M, Bastien J-C, Brignolas F, Marron N.** 2013. Variability and plasticity of productivity, water-use efficiency, and nitrogen exportation rate in *Salix* short rotation coppice. *Biomass & Bioenergy* **56**, 392-404.
- Tschaplinski TJ, Blake TJ.** 1994. Carbohydrate mobilization following shoot defoliation and decapitation in hybrid poplar. *Tree Physiology* **14**, 141-151.
- Tschaplinski TJ, Blake TJ.** 1995. Growth and carbohydrate status of coppice shoots of hybrid poplar following shoot pruning. *Tree Physiology* **15**, 333-338.
- van Laar HH, Goudriaan J, van Keulen H.** 1992. Simulation of crop growth for potential and water limited production situations (as applied to spring wheat). In: CABO-TT, ed. *Simulation Reports*, Vol. 27. Wageningen, The Netherlands: CABO-DLO/Theoretical Production Ecology -Wageningen Agricultural University, 78 pp.
- Verlinden MS, Broeckx LS, Van den Bulcke J, Van Acker J, Ceulemans R.** 2013. Comparative study of biomass determinants of 12 poplar (*Populus*) genotypes in a high-density short-rotation culture. *Forest Ecology and Management* **307**, 101-111.
- Verwijst T, Lundkvist A, Edelfeldt S, Forkman J, Nordh N-E.** 2012. Effects of clone and cutting traits on shoot emergence and early growth of willow. *Biomass and Bioenergy* **37**, 257-264.
- Vivin PH, Castelan M, Gaudillère JP.** 2002. A Source/Sink Model to Simulate Seasonal Allocation of Carbon in grapevine. *Acta Hort. (ISHS)* **584**, 43-56.
- Volk TA, Abrahamson LP, Nowak CA, Smart LB, Tharakan PJ, White EH.** 2006. The development of short-rotation willow in the northeastern United States for bioenergy and bioproducts, agroforestry and phytoremediation. *Biomass & Bioenergy* **30**, 715-727.
- Von Fircks Y, Sennerby-Forsse L.** 1998. Seasonal fluctuations of starch in root and stem tissues of coppiced *Salix viminalis* plants grown under two nitrogen regimes. *Tree Physiology* **18**, 243-249.
- Weih M.** 2009. Genetic and environmental variation in spring and autumn phenology of biomass willows (*Salix* spp.): effects on shoot growth and nitrogen economy. *Tree Physiology* **29**, 1479-1490.
- Weih M, Nordh NE.** 2002. Characterising willows for biomass and phytoremediation: growth, nitrogen and water use of 14 willow clones under different irrigation and fertilisation regimes. *Biomass & Bioenergy* **23**, 397-413.
- Weih M, Nordh NE.** 2005. Determinants of biomass production in hybrid willows and prediction of field performance from pot studies. *Tree Physiology* **25**, 1197-1206.
- Wösten JHM, Lilly A, Nemes A, Le Bas C.** 1999. Development and use of a database of hydraulic properties of European soils. *Geoderma* **90**, 169-185.
- Xu X, Peng GQ, Wu CC, Korpelainen H, Li CY.** 2008. Drought inhibits photosynthetic capacity more in females than in males of *Populus cathayana*. *Tree Physiology* **28**, 1751-1759.



		Average Strength									Rank of strength								
		All WS&NWS	All NWS	All WS	WS R1	WS R2	ABER WS R1+R2	ROTH WS R1+R2	WS END & TN	WS RES & T	All WS&NWS	All NWS	All WS	WS R1	WS R2	ABER WS R1+R2	ROTH WS R1+R2	WS END & TN	WS RES & T
Phenology	C_r	1,535	2451	619	352	886	476	762	782	989	10	9	17	9	19	17	16	21	15
	dl_{BtoBr}	1,866	2967	765	276	1254	355	1176	1344	1165	8	6	13	12	13	22	5	13	12
	dl_{BMax}	1,161	1569	753	104	1402	497	1009	1832	973	15	16	14	24	10	15	10	7	16
	dl_{OSER}	9,184	12083	6285	2441	10129	6641	5929	11941	8317	1	1	1	1	1	1	1	1	1
	f_{fill}	548	876	219	88	351	105	334	449	252	22	20	25	25	25	29	23	24	26
	dd_{fill}	420	539	301	146	456	205	396	588	324	24	22	23	21	23	24	22	23	24
	b_{Rt}	391	0	783	12	1554	765	801	1546	1561	25	34	11	32	9	11	15	11	7
	T_c	686	737	636	173	1098	435	836	1136	1060	20	21	16	19	16	20	14	15	13
Morphology	ρ_{AG}	2,482	4147	816	302	1330	595	1037	1857	803	4	3	10	11	11	13	9	6	18
	h_{ODH}	504	479	529	272	786	451	607	787	785	23	24	20	13	21	18	18	20	19
	C_{LER}	986	1390	581	257	905	570	593	816	995	16	17	19	15	18	14	19	19	14
	m_{LER}	2,011	2669	1354	718	1990	1523	1185	2061	1920	6	8	4	5	4	4	4	5	4
	m_{SER}	2,978	4011	1945	998	2892	1791	2099	3502	2281	2	4	2	3	2	2	3	2	3
	m_{DH}	1,781	2380	1182	751	1614	1248	1117	1788	1439	9	10	6	4	7	6	7	10	8
	NL_{Br}	2,422	3601	1242	498	1986	1331	1153	2062	1910	5	5	5	7	5	5	6	4	5
	$NBuds_o$	658	986	330	257	404	397	264	388	420	21	19	22	16	24	21	25	25	22
	p_{if}	1,381	1760	1001	234	1768	1126	876	1790	1746	12	14	7	18	6	7	13	9	6
	ρ_{Rt}	1,425	1900	949	614	1285	946	953	1206	1364	11	12	9	6	12	8	11	14	10
Light Interception	ff_{max}	844	1089	598	267	930	685	511	1095	765	18	18	18	14	17	12	21	16	21
	k_c	45	69	21	8	34	23	19	45	23	34	31	33	33	33	33	33	33	33
	Ω	1,301	2348	254	32	476	177	331	701	250	13	11	24	28	22	26	24	22	27
	LAI_{cshade}	173	345	1	0	2	1	0	3	0	30	25	35	35	35	35	35	35	35
	SLA_{max}	228	336	121	84	159	119	124	203	115	28	26	28	26	30	28	28	28	29
	SLA_{min}	39	50	29	18	39	31	26	46	31	35	32	32	31	32	31	32	32	32
	η	835	1577	94	22	166	71	117	265	68	19	15	30	29	29	30	29	26	30
Physiology	ρ_{20}	208	223	193	110	277	225	162	176	378	29	27	26	23	26	23	27	30	23
	φ_{pot}	2,683	4655	710	254	1166	491	930	1465	867	3	2	15	17	14	16	12	12	17
	A_{max}	1,189	1866	512	168	856	444	580	941	772	14	13	21	20	20	19	20	18	20
	μ_T	1,938	2902	974	342	1607	869	1080	1813	1401	7	7	8	10	8	9	8	8	9
	μ_{shade}	50	98	2	0	4	3	1	8	0	33	30	34	34	34	34	34	34	34
	μ_{WS}	384	0	767	431	1103	792	743	1001	1206	26	33	12	8	15	10	17	17	11
	$d_{AfterCut}$	363	537	189	144	233	202	175	210	256	27	23	27	22	27	25	26	27	25
	Res_{max}	157	196	118	35	200	139	96	191	210	31	28	29	27	28	27	30	29	28
	μ_W	96	159	34	20	48	25	43	63	33	32	29	31	30	31	32	31	31	31
	WSP	972	0	1944	1128	2760	1706	2182	2400	3120	17	34	3	2	3	3	2	3	2

